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Adres redakcji: Instytut Systematyki i Ewolucji Zwierząt Polskiej Akademii Nauk,
ul. Sławkowska 17, 31-016 Kraków

Address of the Editor: Institute of Systematics and Evolution of Animals,
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The FIRST INTERNATIONAL SYMPOSIUM on TIPULOMORPHA:
SYSTEMATICS and PHYLOGENY
Kraków, 9-13. September, 1991.

This issue of *Acta zoologica cracoviensia* contains exclusively the proceedings of the symposium, which was held in the Academy's Conference Centre - Mogilany, 20 km south of Kraków and assembled 20 specialists from 11 countries: Japan, USA, USSR, Lithuania, Poland, Czechoslovakia, Germany, Switzerland, Netherlands, Sweden and Great Britain.

During the meeting we hoped to reach a consensus on one taxonomic system of Tipulomorpha and to adopt one uniform system of wing venation nomenclature. That we did not succeed (this time) is apparent when one compares the papers of: J. STARY, H. PRATT, W. KRZEMIŃSKI and T. TORIL. The hot atmosphere of the symposium is reflected in the following summary written by Alan STUBBS.

Since some lectures were not submitted for publication in the Proceedings, all the titles are listed below:

1. George BYERS (USA): Comments on the ALEXANDER's system: one versus three families (read by J. GELHAUS).

2. Christine DAHL (Sweden): Character evaluation in developmental stages of Tipulomorpha (not submitted).

3. Christine DAHL: *Kawasemyia*, an invalid genus and Kawasemyiinae, an invalid subfamily of Trichoceridae (Diptera, Nematocera).

4. Christophe DUFOUR (Switzerland): The alpine and subalpine Tipulidae in Switzerland. Morphology, ethology, ecology and distribution (Diptera, Nematocera).

5. Jon GELHAUS (USA): The importance of characters of the female genitalia for understanding the systematic relationships of the Tipulomorpha (not submitted).

6. Ewa KRZEMIŃSKA (Poland): Morphometric study of wing venation in the recent Trichoceridae - an application to the fossils?

7. Ewa KRZEMIŃSKA (Poland): Paracladurinae - new subfamily within the Trichoceridae.

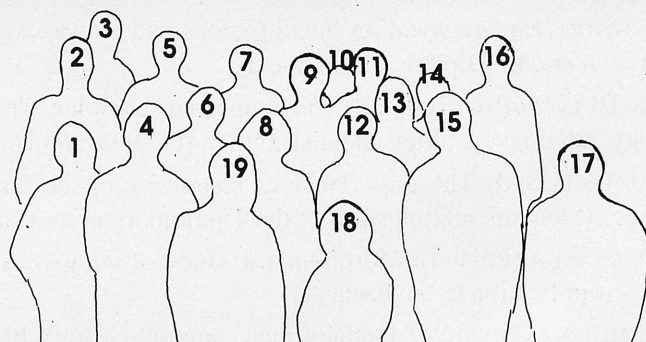
8. Wiesław KRZEMIŃSKI (Poland): Fossil Tipulomorpha and their importance to the phylogeny of the group.

9. Wiesław KRZEMIŃSKI (Poland): Limoniidae (Diptera, Nematocera) from Dominican amber. I. Genus *Molophilus* CURTIS, 1833.

10. Wiesław KRZEMIŃSKI, Giuseppe GENTILINI (Italy): Fossil Limoniidae from Monte Castellaro (Central Italy, Upper Miocene).

11. Volodia LANTSOV (USSR): Primitive features of Tipulomorpha and their significance for the group in extremal conditions.

12. Pjotr OOSTERBROEK (Netherlands): On characters of larvae and pupae of Tipuloidea and their implications on the phylogeny of the major groups of Tipuloidea and on the position of the Tipuloidea within the Nematocera. (in press: Phylogeny of the Tipuloidea based on characters of larvae and pupae (Diptera, Nematocera), with an index to the



Mogilany, September, 1991.

- | | |
|------------------------------------|-------------------------------------|
| 1 - Chen W. Young, USA | 11 - Jolanta Wiedeńska, Poland |
| 2 - Hermann de Jong, Netherlands | 12 - Jaroslav Stary, Czechoslovakia |
| 3 - Sigitas Podenas, Lithuania | 13 - Herbert Reusch, Germany |
| 4 - Pjotr Oosterbroek, Netherlands | 14 - Jon Gelhaus, USA |
| 5 - Takashi Torii, Japan | 15 - Willy Geiger, Switzerland |
| 6 - Volodia Lantzov, Russia | 16 - Jane Stubbs, Great Britain |
| 7 - Alan Stubbs, Great Britain | 17 - Tadeusz Zatwarnicki, Poland |
| 8 - Christine Dahl, Sweden | 18 - Ewa Krzemińska, Poland |
| 9 - Christophe Dufour, Switzerland | 19 - Wiesław Krzemiński, Poland |
| 10 - Elżbieta Skalska, Poland | |

literature except Tipulidae. P. OOSTERBROEK & Br. THIEOWALD. Tijdschrift voor Entomologie, 1991).

13. Pjotr OOSTERBROEK (Netherlands): On area cladograms of Mediterranean Tipulidae in relation to the palaeogeography of the Mediterranean region. (in press: Area-cladograms of circum-Mediterranean taxa in relation to Mediterranean Palaeogeography. P. OOSTERBROEK & J.W. ARNTZEN. Journal of Biogeography, 1992).

14. Sigita PODENAS (Lithuania): Tipulidae, Limoniidae, Cylindrotomidae, Trichoceridae and Ptychopteridae of Lithuania.

15. Jaroslav STARÝ (Czechoslovakia): Phylogeny and classification of Tipulomorpha with special emphasis on the family Limoniidae.

16. Alan STUBBS (Great Britain): The crane fly recording scheme in the British Isles; mapping, biotope studies and application to conservation objectives.

17. Takashi TORII (Japan): Systematic study of the subtribe Antocharia mainly based on male and female terminalia. (Diptera, Tipulidae, Limoniinae).

18. Chen W. YOUNG (USA). Jon GELHAUS: *Leptotarsus (Longurio) byersi*, a new flightless crane fly from Ecuador (Diptera: Tipulinae).

In this volume are also included some papers that were not presented at the symposium but submitted for publication afterwards.

Acknowledgements:

The symposium and the publisher's costs were in great part covered by two institutions: the Biological Division of the Polish Academy of Sciences (Warszawa) and the Institute of Systematics & Evolution of Animals, Polish Academy of Sciences (Kraków) to whom the organizers are deeply indebted. We would like also thank the Editorial Board of Acta Zoologica Cracoviensia for their help in publishing this volume.

Organizers:

Ewa KRZEMIŃSKA and Wiesław KRZEMIŃSKI

Institute of Systematics & Evolution
of Animals, Polish Academy of Sciences,
ul. Sławkowska 17, Kraków, Poland.

The First International Symposium on Tipulomorpha
Systematics and Phylogeny.
Kraków, Poland, 9-13. September, 1991.

Alan STUBBS

A party of 20 specialists in craneflies assembled in Kraków from eleven countries: Japan, USA, USSR, Lithuania, Germany, Poland, Czechoslovakia, Switzerland, Netherlands, Sweden and Great Britain. The symposium hosts were Drs Ewa & Wiesław KRZEMIŃSKI of the Polish Academy of Sciences, and we stayed at the Academy's XIX century mansion at Mogilany, about 20 km south of Kraków.

The symposium opened with recognition of the great part that the late Charles P. ALEXANDER played in advancing taxonomic knowledge of craneflies, having described 10,000 species new to science. Later, a resolution was made, addressed to the American Science Foundation, seeking assistance to the Smithsonian Institution for the curation of ALEXANDER's collection and notes.

The Symposium was especially concerned with some phylogenetic problems that needed resolution, if possible, in the time for the forthcoming Palaearctic catalogue to Tipulomorpha. Thus the first major presentation reviewed characters and outlined a cladogram (J. STARÝ). The Trichoceridae were considered a primitive, relict group, with Tipulidae, Limoniidae and Cylindrotomidae as separate families, and indeed there was a good case for dividing off another family, Pediciidae. Larval and pupal characters, and more cladograms tended to reveal problems arising as a result of characters not being necessarily unique within the above families (P. OOSTERBROEK). To round off the opening session and to ensure all options were in mind, the argument for a single family Tipulidae (apart from Trichoceridae) was presented (J. GELHAUS on behalf of George BYERS). The single family concept was a historic one upheld by ALEXANDER in the USA (with support from the late F.W. EDWARDS of Great Britain) whilst European workers have long favoured a separation into 3 families.

A strong argument was made for a greater concern for female genitalia characters (J. GELHAUS). Though there are adaptations to oviposition strategy, on the whole the higher level ground plan was much more constant than found in larval features and male genitalia. This much neglected matter needs further study.

The fossil records were reviewed by our hosts. The first known Tipulomorpha are found in the Upper Triassic of the USA (Limoniidae) and Trichoceridae from the Lower Jurassic. Later deposits in Dominica and Europe gave a certain record through the Mesozoic and Tertiary, the famous Baltic amber including very modern looking material. The Tipulidae s.s. were first found in the Cretaceous, but there was a big radiation of recent genera of this and Limoniidae in the Tertiary. Thus it was confirmed that Trichoceridae are a very old group and much consideration of the evolution of this family was presented. Also the use of wing venation characters in studying the fossils was discussed (E. KRZEMIŃSKA).

One of the big issues was whether Trichoceridae should be placed with the Tipulomorpha or, as has been advocated by some workers, in the Psychodomorpha. As became increasingly clear from several speakers, the adult characters have much in common with Tipulidae yet some larval features are more similar to those of the Psychodomorpha. In the end an impromptu evening debate decided that Trichoceridae should be treated as Tipulomorpha, though whether Tipulidae should be regarded as one, three or four families evaded unanimous resolution.

A more detailed look at various modern genera helped focus on some of the more detailed problems facing the taxonomist. The genus *Antocha* in Japan and the related West Pacific area demonstrated that the traditional subgeneric concepts did not hold. (T. TORII). Now that more species are known in the female as well as the male, the subgenus *Proantocha* has to be narrowed to two species whose subgeneric characters hold in both sexes. A number of equally relevant sub-groupings could be accorded equal subgeneric status if *Proantocha* and s.s. *Orimargula* are still to be recognized. Among various genera that were considered, there was a puzzling species of a genus from the high Andes of Ecuador (C. YOUNG) that did not provoke an eager rush of solutions from the phylogeneticists.

Though the title of the symposium was seemingly restricted, there were several papers more concerned with ecological and distribution matters. Thus we learnt that the fauna of the northern fringe of the Russian tundra had various ecological adaptations, including the fact that the tipulids are major pollinators in the environment and they maintain a 24hr activity rhythm in almost uniform 24 hr daylight (V. LANTSOV). The alpine fauna of Switzerland was reviewed (C. DUFOUR) and the Lithuania fauna was outlined (S. PODENAS). The geological evolution of the Mediterranean basin and the nature and origin of the Tipulidae (s.s.) fauna gave an interesting view of past and contemporary ecologies and distribution patterns. The nature and history of the crane-fly recording scheme in the British Isles was outlined, including its application to conservation objectives (A. STUBBS).

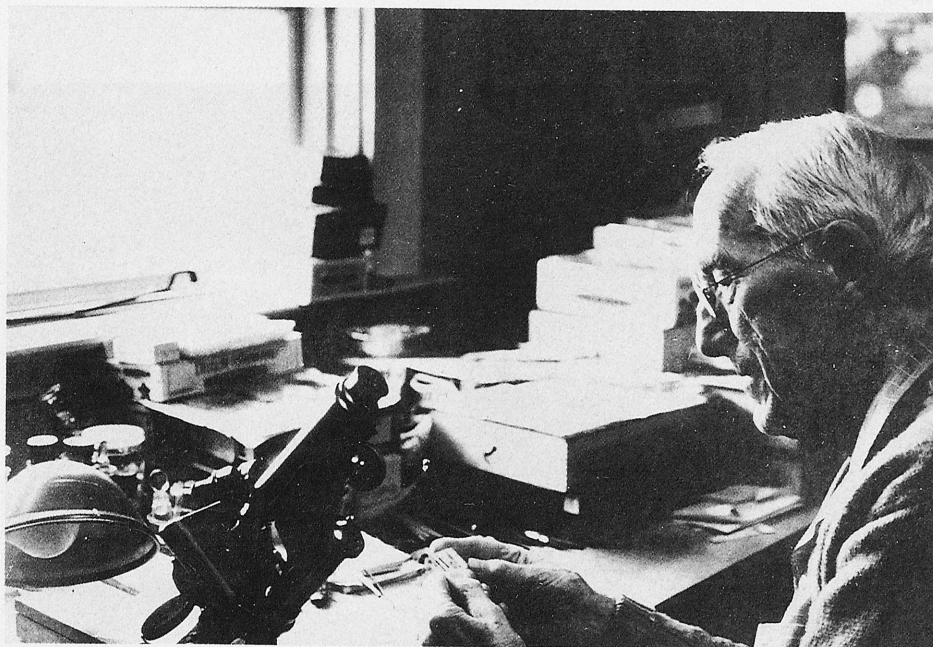
There was time for some sightseeing in Kraków and a boat trip on the Dunajec river. Some of the party stayed on for a collecting trip into the Tatra mountains and a few also visited some other areas in south-east Poland.

Our hosts were warmly congratulated on the great success of the symposium and another is to be held in the Netherlands in three years time.

181 Broadway, Peterborough,
PE1 4DS, Great Britain

Memories of Crane-Fly Heaven

Christine DAIL



C. P. ALEXANDER in his studio.

When I was a not any more so young student I made my first contributions to taxonomy by working on the European winter gnat species in the family Trichoceridae. And every time I checked material from outside Europe there was the same name, ALEXANDER, on the species. This specialist had described new species from all continents and especially concentrated on writing catalogues of American faunas. Given our faunal connections in the Holarctic I simply had to write to him about some problems. I got the most comprehensive and courteous letters back. For many years this so very useful correspondence went on. My plans to achieve a world catalogue on Trichoceridae gradually grew, and I wrote a letter asking Dr ALEXANDER if he would be so kind to coauthor it. He answered he would be delighted to be my junior author. That was about 1975, when Dr ALEXANDER had already put behind him a little more than 80 years of his industrious life.

A year later I had the opportunity to visit him and his wonderful wife Mabel in Amherst, Massachusetts. I really could experience at first hand that deep human humour which was underlying his answer to my question of coauthorship. Both ALEXANDERS had this gift of seeing the humorous and, if necessary, even absurd angle in an every-day situation. They had kept it also over the period Dr ALEXANDER lost his first tipulid collection when their home had burned down. Dr ALEXANDER retired in his Fifties from his professorship

to rebuild his lost collection. He devoted himself to the study of Tipulomorpha and built a world collection of all genera and as many species as possible. If I remember right from a stiched map over the ALEXANDERS' mantel piece, they had gone at least 12 times across the Northamerican continent from coast to coast in their car. Driving, as well as typing and other secretarial matters was the section of Mabel ALEXANDER in the crane-fly business.



Mabel and Charles ALEXANDER. 1976, Amherst, Mass.

At the end of his career Dr ALEXANDER had published over thousand articles with descriptions, mainly based on males, and distributions of newly described species. The collection and his small studio formed a marvellous little museum. His brass microscope with an aperture of polished turtle carapace and an old hand-made German lens was also a museum article, inherited from his predecessor Dr FERNALD. Every species was card indexed and a relevant library completed the set up. Around ten thousand species were named by him and the amount of synonyms is still very low. The ALEXANDERS had added a wooden anex to their wooden New English home and called it Crane Fly Heaven. There was a thunderstorm at night during my visit and, alerted by previous experiences, we were wide awake and prepared to fight fire.

Dr ALEXANDER was a practical man and saw the difficulties of publishing taxonomic work. He thus accordingly made a donation for a publishing fund tied to the Annals of the Entomological Society of America and bequested his collection to the Smithsonian, Washington D. C. Everybody working with adult crane-flies will have to consult this collection. To tie the other life stages to the species described, or to do systematics and

evolutionary studies on higher taxa in the Tipulomorpha will also need access to the ALEXANDER collection. The name ALEXANDER is for ever a symbol for outstanding and most extensive work on the Tipulomorpha. For us who had the fortune to know the ALEXANDERS as persons, there always will be so much more to remember than an author name to a crane-fly species.

Section of Entomology,
Department of Zoology,
Box 561, S-751 22
Uppsala, Sweden

Phylogeny and classification of Tipulomorpha, with special emphasis on the family Limoniidae

Jaroslav STARÝ

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STARÝ J. 1992. Phylogeny and classification of Tipulomorpha, with special emphasis on the family Limoniidae. Acta zool. cracov., 35(1): 11-36.

Abstract: Phylogeny and classification of higher taxa of the Tipulomorpha are discussed, based on an analysis of adult morphological characters of recent species. The proposed conception excludes the subfamily Pediciinae from the Limoniidae and raises it to full family rank. The genus *Dactylolabis* is assigned the rank of subfamily. Thus, the infraorder Tipulomorpha is classified in five families, the Trichoceridae, Pediciidae, Tipulidae, Cyliodromidae and Limoniidae, the latter with the subfamilies Dactylolabinae, Hexatomininae, Eriopterinae and Limoniinae.

Key words: Tipulomorpha, phylogeny, classification, adult characters.

Jaroslav STARÝ, Department of Zoology, Natural Sciences Faculty of the Palacký University, tř. Svobody 26, 771-46 Olomouc, Czechoslovakia.

INTRODUCTION

Numerous classificatory schemes have been proposed to show affinities of main groups and subgroups of the Tipulomorpha but, since HENNIG, relatively little has been done as far as phylogeny of the infraorder is concerned. Of the two major families, the Tipulidae and Limoniidae, considerably more attention, in this respect, has been paid to the former.

The works by THEOWALD (1957) and FROMMER (1963) were phylogenetic in scope, containing comparative morphology, but did not outline any schemes to show phylogenetic relationship. SAVCHENKO (1966) discussed phylogeny of the subgroups within the Tipulidae and provided particular diagrams, based on both larval and adult characters. Later, phylogeny of the genus *Nephrotoma* and its *dorsalis* species group was worked out by OOSTERBROEK (1980) and TANGELDER (1985) respectively, with particular cladograms supported by a proper cladistic analysis. The same was done by THEOWALD (1984) as regards the subgenus *Tipula* s.str. and by BRODO (1987) for the genus *Prionocera*.

As to the Limoniidae, only recently, SAVCHENKO (1986) presented a systematic arrangement that may be considered phylogenetic. This scheme, setting apart the subfam-

ily Pediciinae as the sister group of the other subfamilies of the Limoniidae and reducing eventually the rank of the latter subfamilies (viz. Hexatominiae, Eriopterinae, Limoniinae) to supertribes under the superordinate term Limoniinae sensu lato, indicated, in a certain respect, what is expressed in more detail here. A shortcoming in approach is now becoming generally evident resulting from the fact that only single families in a traditional sense have been considered, with no regard for other groups of the Tipulomorpha. A phylogenetic classification of the families Cylindrotomidae, Tipulidae and Limoniidae, based on preimaginal characters, was suggested by OOSTERBROEK (1986). In printed form, however, it was presented as summary only, without any argumentation, and is to be regarded as preliminary.

In the present paper, the phylogeny and classification of higher taxa of the Tipulomorpha are discussed, based on an analysis of adult morphological characters. Mostly ground plan characters are employed. In some cases, apomorphic character states not belonging to the ground plan of the groups under consideration are discussed. Their shared possession, indicating parallel evolution, may, however, serve as auxilliary evidence (so-called underlying synapomorphy; cf. SAETHER 1979).

The infraorder Tipulomorpha is conceived here according to HENNIG (1954 and subsequent papers), comprising originally four families of Diptera, the Trichoceridae, Tipulidae, Cylindrotomidae and Limoniidae. The Trichoceridae are considered to form the sister group of the remaining Tipulomorpha. The latter are thought to have evolved along two phylogenetic lines. The one comprises the Tipulidae, Cylindrotomidae and one subfamily of the Limoniidae, the Pediciinae, with the sister groups Pediciinae and Tipulidae + Cylindrotomidae. The other line, the Limoniidae (in a restricted sense), is considered here at subfamily level. The genus *Dactylolabis* is suggested as the most primitive offshoot of the family. The remaining Limoniidae appear to form the sister groups Hexatominiae and Eriopterinae + Limoniinae (cf. Fig. 35).

The present conception excludes the subfamily Pediciinae from the Limoniidae and raises it to full family rank. Thus, the infraorder Tipulomorpha is classified here in five families, the Trichoceridae, Pediciidae, Tipulidae, Cylindrotomidae and Limoniidae. The genus *Dactylolabis* is assigned the rank of subfamily. Thus, the Limoniidae, as delimited here, comprise the subfamilies Dactylolabinae, Hexatominiae, Eriopterinae and Limoniinae.

Although the present paper is a result of my own studies and reflects my own views, I would like to thank all participants of the First International Symposium on Tipulomorpha, held in Kraków in September 1991. The discussions with them on the subject were highly fruitful and inspiring for me. I am grateful to Mr. V. KUBAK (Natural Sciences Faculty of the Palacky University, Olomouc) for technical assistance.

MONOPHYLY OF TIPULOMORPHA

As already mentioned in the introduction, the present concept of the Tipulomorpha involves also the family Trichoceridae. The larval characters, on the basis of which some doubts had been raised as to assignment of the Trichoceridae to this infraorder (CRAMPTON

1926; EDWARDS 1928), were considered to represent plesiomorphic states that could not show phylogenetic relationship (HENNIG 1954; DAHL and ALEXANDER 1976).

It was not the original aim of this paper to examine the monophyly of the Tipulomorpha. Attention is paid here, above all, to the cladistic analysis of the families, with notable emphasis on the Limoniidae, and the above monophyly actually was taken for granted. Since, however, repeated attempts have occurred recently, based again mainly on larval characters, to segregate the Trichoceridae from the Tipulomorpha and to relate them with the Anisopodidae (KRIVOSHEINA 1988; WOOD and BORKENT 1989), the problem is commented here in some detail. It may be symptomatic that solely non-specialists on the infraorder claim this, solely on larval characters.

An extensive treatment was provided by WOOD and BORKENT (1989), in the Manual of Nearctic Diptera, volume 3, supporting the removal of the Trichoceridae from the Tipulomorpha. I am not able, at the moment, to judge the larval details suggested by the authors as the basis for grouping the Trichoceridae with their Psychodomorpha. I can only presume that, if they really are apomorphic and homologous, these characters represent convergences as a result of parallel selection which especially larval stages are largely subject to.

However, comments are provided here for the benefit of some of the characters on which HENNIG established his concept of Tipulomorpha, as enumerated, discussed and rejected as plesiomorphic or misinterpreted by WOOD and BORKENT (1989).

(A) All branching points of longitudinal veins distalized.

This feature is actually identical with that proposed originally by HENNIG (1968). In the above somewhat modified phrasing it is considered here a clear apomorphy. The character state appears rather relative but a comparison of various venational patterns within and outside the Tipulomorpha revealed unambiguously its justification as a ground plan synapomorphy of the infraorder. In the Tipulomorpha, branching points of longitudinal veins are shifted distinctly more distally in comparison with both what is considered the ground plan of the Diptera and the condition in representatives of non-tipulomorphan families. Mostly, they are situated beyond the middle of wing but some may not be (eg. R_1 - R_s). It should be emphasized that only branching points are considered, not connections of longitudinal veins with the costa. The evolutionary trend of the latter points is different in Tipulomorpha (see "Characters" under (1)). Distalization of branching points also affects the position of the discal cell which likewise is shifted more distally. Such a venational pattern is not likely to be related to the width of wing. In the Trichoceridae, for instance, wings are broader than in most other nematoceran families, yet distalization of branching points is quite apparent. This character state does not seem to be paralleled in ground plans of any of the other dipteran infraorders.

(B) Vein R_2 fused with R_1 distally, not reaching wing margin as a separate vein.

This again is considered here a synapomorphy of all the families of the Tipulomorpha, including the Trichoceridae. As a reply to some doubts raised

by WOOD and BORKENT (1989) as to the correct interpretation of R₂ and its homology in the Trichoceridae and the rest of Tipulomorpha, the following should be stated. Detailed examination of wing venation in many groups and subgroups of the Tipulomorpha revealed that setae tend to atrophy on all vertical elements, including verticalized longitudinal veins or their parts (also on vertical apical portion of A₂ in *Trichocera* s.str.*). If vertical in position, R₂ usually lacks setae both in the Trichoceridae and, in contrast to the statement by WOOD and BORKENT, in the remaining Tipulomorpha, and its homology in the two groups seems beyond any doubt. Distal fusion of R₂ with R₁, the so-called cephalization of R₂ (ALEXANDER 1927), and its verticalization is in accordance with principal tendencies in the evolution of wing venation, as outlined in "Characters" under (1). Variation in position of the verticalized R₂ may be explained as a result of proximalization of vertical elements which likewise appears to be a trend in the Tipulomorpha. As support for the correct interpretation of R₂ the fact should be mentioned that once the verticalized R₂ atrophied, which frequently occurred (e.g., in eriopterine Limoniidae), an analogous process of cephalization is detectable for the next longitudinal vein, namely R₃. This vein likewise may become vertical and fuse, in some cases, distally with R₁. Thus, cephalization of R₃ is completed, the position of participating veins being identical with, and convergent to the state described above. Such venational patterns are observable in the genera *Atarba* and *Idiocera* (Limoniidae: Eriopterinae).

Two further features appear to be apomorphic for the Tipulomorpha and should be thoroughly examined:

(C) Wing base strongly narrowed.

This definitely does not depend on overall outline of the wing. Rather the character could be correlated with the manner in which wings are folded at rest in the Tipulomorpha.

(D) Veins M, M₃₊₄ and M₄ in alignment (discal cell above the stem M).

The above complex of non-adaptive and possibly correlated, apomorphic ground plan character states is considered here to have sufficiently high weight to support the monophyly of the Tipulomorpha, including the Trichoceridae. In addition, the way in which the meron is reduced in the Tipulomorpha may be a good underlying synapomorphy (see closing paragraphs in "Characters"). Anyway, the concept of the Tipulomorpha, as proposed by HENNIG, still seems to be the best hypothesis.

*From the relevant paragraph on the character, by WOOD and BORKENT (1989), doubting even the homology of A₂ (as regards the apex of the vein) in the Trichoceridae and the rest of Tipulomorpha, an impression can arise that the abruptly bent apical portion of A₂ is generally distributed in the family. However, the feature is significantly pronounced in a single subgenus, though the one richest in species, viz. *Trichocera* s.str. In most other taxa (*Metatrachocera*, *Diazosma*, *Paracladura*), the course of the vein is much shallower. In *Diazosma*, for instance, setae do continue to the apex of the vein.

Finally, I feel also a statement should be added as to the sister group of the Tipulomorpha. In my opinion, this is either the rest of the Diptera, or the Psychodomorpha sensu HENNIG, but in no case the remaining Nematocera.

CHARACTERS

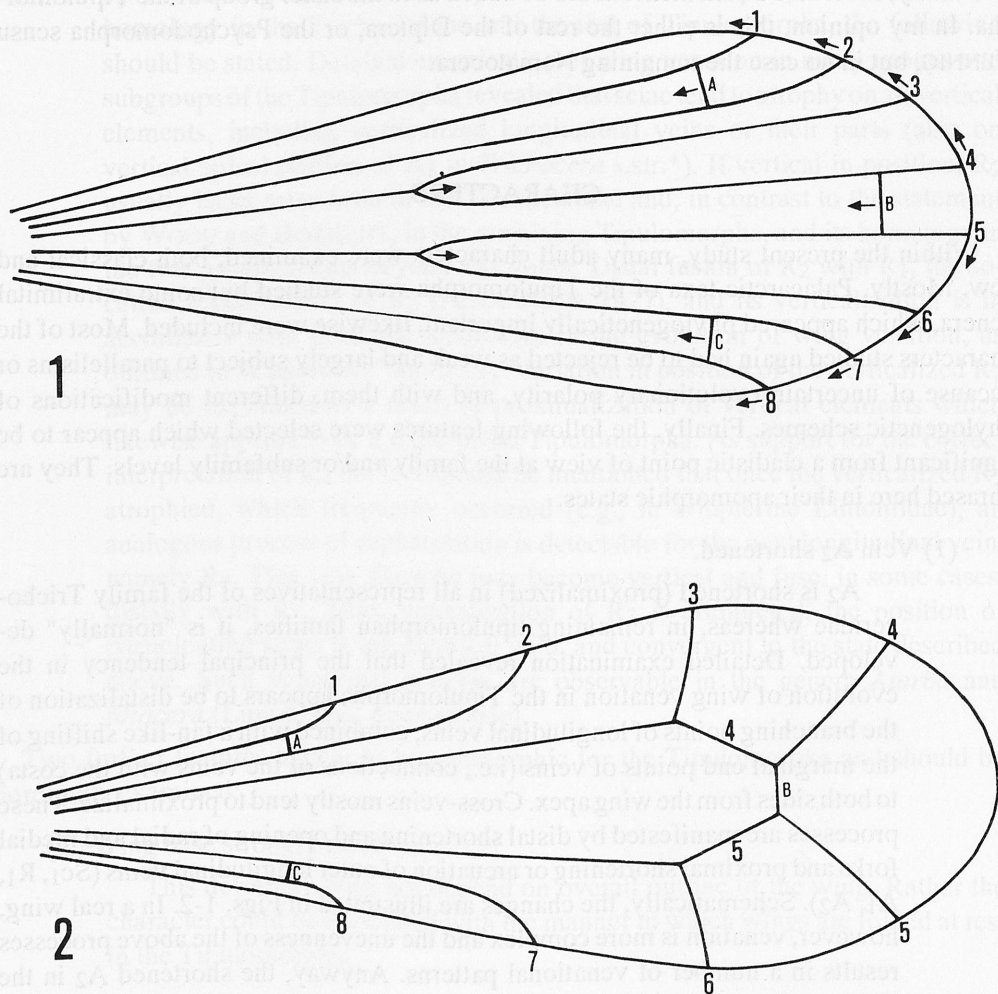
Within the present study, many adult characters were examined, both classical and new. Mostly, Palearctic taxa of the Tipulomorpha were studied but some extralimital genera, which appeared phylogenetically important, likewise were included. Most of the characters studied again had to be rejected as weak and largely subject to parallelisms or because of uncertain evolutionary polarity, and with them, different modifications of phylogenetic schemes. Finally, the following features were selected which appear to be significant from a cladistic point of view at the family and/or subfamily levels. They are phrased here in their apomorphic states.

(1) Vein A₂ shortened.

A₂ is shortened (proximalized) in all representatives of the family Trichoceridae whereas, in remaining tipulomorphan families, it is "normally" developed. Detailed examination revealed that the principal tendency in the evolution of wing venation in the Tipulomorpha appears to be distalization of the branching points of longitudinal veins, combined with a fan-like shifting of the marginal end points of veins (i.e., connections of the veins with the costa) to both sides from the wing apex. Cross-veins mostly tend to proximalize. These processes are manifested by distal shortening and opening of radial and medial forks and proximal shortening or arcuation of outer longitudinal veins (Sc₁, R₁, A₁, A₂). Schematically, the changes are illustrated in Figs. 1-2. In a real wing, however, venation is more complex and the unevenness of the above processes results in a number of venational patterns. Anyway, the shortened A₂ in the Trichoceridae coincides with the principal tendencies and is therefore considered an apomorphy. In a few specialized taxa outside the Trichoceridae, A₂ likewise became shortened, having sometimes partly fused to the posterior border of wing (Limoniidae: *Pseudoglochina*), or even atrophied (Cylindrotomidae: *Stibadocerella*; Limoniidae: *Doaneomyia*) (perhaps actually entirely fused to the costa). However, these parallelisms cannot be regarded as ground plan characters at family or subfamily levels.

(2) Free cardo absent.

Within the Tipulomorpha, the basal part of the maxilla, the cardo, ca, is present as a separate segment in the Trichoceridae only and this condition is regarded as plesiomorphic. The cardo has the appearance of a short pigmented rod directed laterally, at about the right angle to the stipes, sti, its outer end being associated with the invagination of the posterior arm of the tentorium (Fig. 3). Cardines are not distinguishable in any of the remaining tipulomorphan

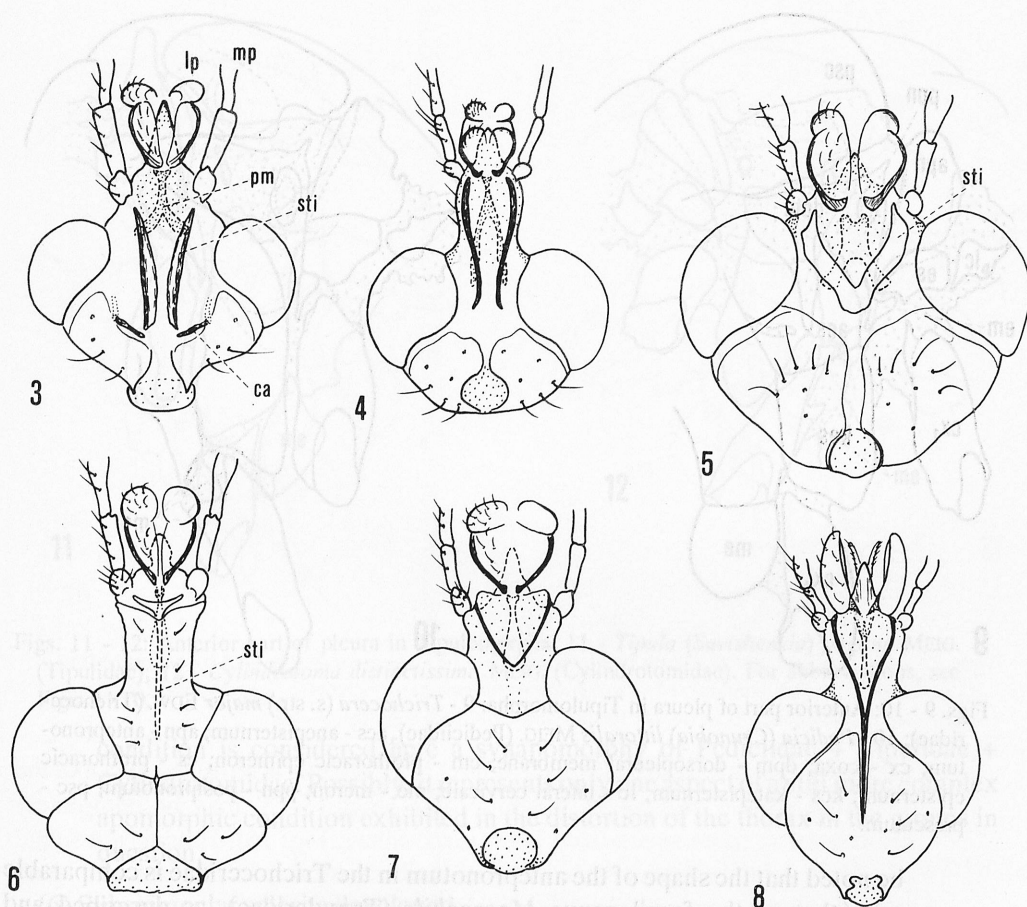


Figs. 1 - 2: Schematic illustrations showing the principal tendencies in evolution of wing venation in Tipulomorpha.

families. They are either atrophied or entirely fused to stipites (cf. Figs. 4-8). This condition is considered a synapomorphy of the rest of the Tipulomorpha.

(3) Ocelli absent.

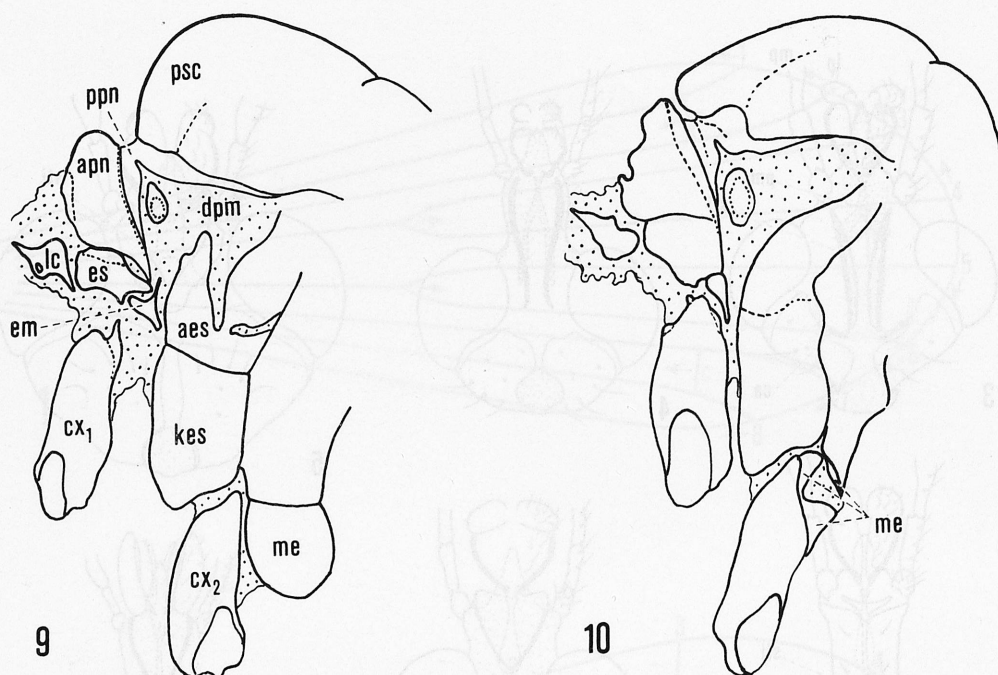
Presence of three ocelli is a ground plan character of the Diptera and so it is as regards to the Tipulomorpha. In the Trichoceridae, ocelli are present what undoubtedly represents the plesiomorphic state. Absence of ocelli is a synapomorphy of the remaining families of the infraorder although something like an ocellar tubercle may still be observed in scattered taxa and might perhaps be of some value when relationships at lower levels are considered.



Figs. 3 - 8: Mouthparts of Tipulomorpha: 3 - *Trichocera* (s. str.) *major* EDW. (Trichoceridae); 4 - *Ula* (s. str.) *bolitophila* LOEW (Pediidae); 5 - *Dicranota* (s. str.) *bimaculata* SCHUMM. (Pediidae); 6 - *Tipula* (*Savtshenkia*) *pagana* MEIG. (Tipulidae); 7 - *Euphyllidorea fulvonervosa* SCHUMM. (Limoniidae: Hexatomiinae); 8 - *Limonia macrostigma* SCHUMM. (Limoniidae: Limoniinae). ca - cardo; mp - maxillary palpus; pm - prementum; sti - stipes.

(4) Antep pronotum elongate, flattened.

The pronotum of the Tipulomorpha, like that of other Diptera, is divided into an anterior region, antep pronotum, apn, and a posterior region, postpronotum, ppn (Fig. 9). The two parts are separated by a transnotal suture, continued downwards between the prothoracic episternum, es, and the epimeron, em. Generally, the antep pronotum is heavily sclerotized and somewhat convex dorsally while the postpronotum is depressed and, as a rule, less sclerotized. In the Pediciidae, Tipulidae and Cylindrotomidae, the antep pronotum is relatively short, strongly elevated, and often collar-shaped (Figs. 10-12). In most Limoniidae, it is elongate and flattened (Figs. 13-16). In the Trichoceridae, the condition is somewhat intermediate between the two states (Fig. 9). It should

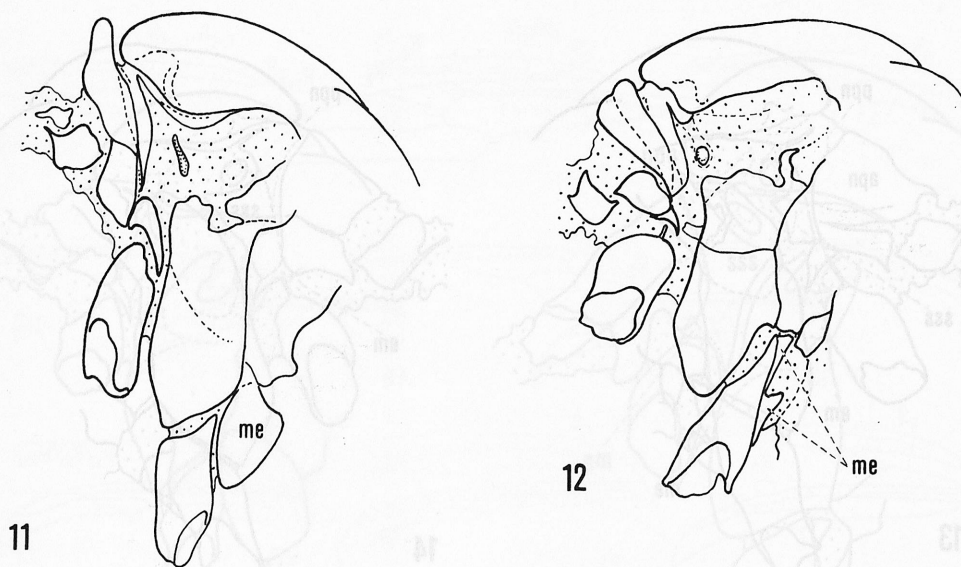


Figs. 9 - 10: Anterior part of pleura in Tipulomorpha: 9 - *Trichocera* (s. str.) *major* EDW. (Trichoceridae); 10 - *Pedicia* (*Crunobia*) *littoralis* MEIG. (Pediidae). aes - anepisternum; apn - antepronotum; cx - coxa; dpm - dorsopleural membrane; em - prothoracic epimeron; es - prothoracic episternum; kes - katepisternum; lc - lateral cervicale; me - meron; ppn - postpronotum; psc - prescutum.

be noted that the shape of the antepronotum in the Trichoceridae is comparable with that of the fossil genus *Macrochile* (Tanyderidae), as described and illustrated by CRAMPTON (1926) and considered by him an ancestral condition. Similarly, the character state in the Trichoceridae may be regarded as plesiomorphic. Hence, the elongate and flattened antepronotum in the Limoniidae (Figs. 13-16) is considered here an apomorphic condition, although sometimes secondarily reduced (especially in the groups of genera centering around *Hexatoma* (Hexatominae), *Gonomyia* (Eriopterinae) and *Antocha* (Limoniinae)).

(5) Postpronotum impressed dorsally, a deep cleft between antepronotum and prescutum.

Another apomorphic manifestation of the character described above occurs in the Pediidae, Tipulidae and Cylindrotomidae. In these families, the postpronotum is reduced and strongly impressed dorsally leaving a deep cleft between the antepronotum and the prescutum (Fig. 10-12). Actually, all the three above-mentioned sclerites contribute to this complex feature becoming compressed frontally; the antepronotum is shortened and strongly elevated, sometimes conspicuously collar-shaped, the postpronotum strikingly impressed and the prescutum again protruding and somewhat truncate at its anterior margin. The cleft between antepronotum and prescutum is continued in the transnotal suture, which likewise is deeply infolded. The described

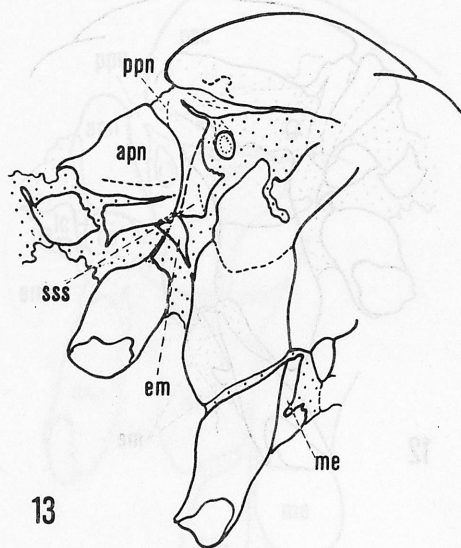


Figs. 11 - 12: Anterior part of pleura in Tipulomorpha: 11 - *Tipula (Savtshenkia) pagana* MEIG. (Tipulidae); 12 - *Cylindrotoma distinctissima* MEIG. (Cylindrotomidae). For abbreviations, see Figs. 9 - 10.

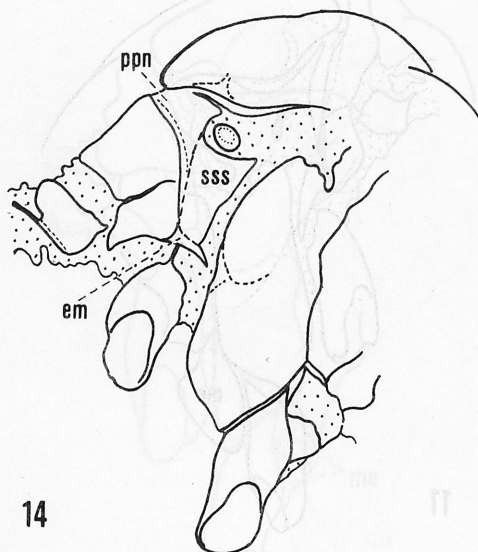
condition is considered here a synapomorphy of Pediciidae + Tipulidae + Cylindrotomidae. Possibly, it represents only one aspect of a still more complex apomorphic condition exhibited in the distortion of the thorax in the groups in question.

(6) Subspiracular sclerite developed.

From dorsal area between the antep pronotum, apn, and the prescutum, psc, the postpronotum, ppn, is continued posteriorly along the lateral margin of the prescutum to form the so-called humerus, or paratergite. In addition, it emits another strip-like extension downwards along the transnotal suture that narrows inferiorly, ending above or touching the prothoracic epimeron, em (Figs. 9-12). This element, although probably belonging to the propleuron, is here referred to as the pleural part of the postpronotum. It proved to be of considerable value as far as phylogeny of the Tipulomorpha is concerned. Posterior to it, a large, roughly triangular membranous area spreads in the antero-superior region of the mesothoracic pleura, the so-called dorsopleural membrane, dpm. The described condition occurs in the Pediciidae, Tipulidae and Cylindrotomidae (Figs. 10-12) and since present also in the outgroup, the Trichoceridae (Fig. 9), it is likely to represent the plesiomorphic state. On the other hand, in the Limoniidae, the pleural part of the postpronotum is greatly enlarged posteriorly by a sclerotized area that extends into the dorsopleural membrane, approaching the anepisternum, aes, and leaving a membranous enclave for the mesothoracic spiracle. The latter is positioned more superiorly than in the other families.



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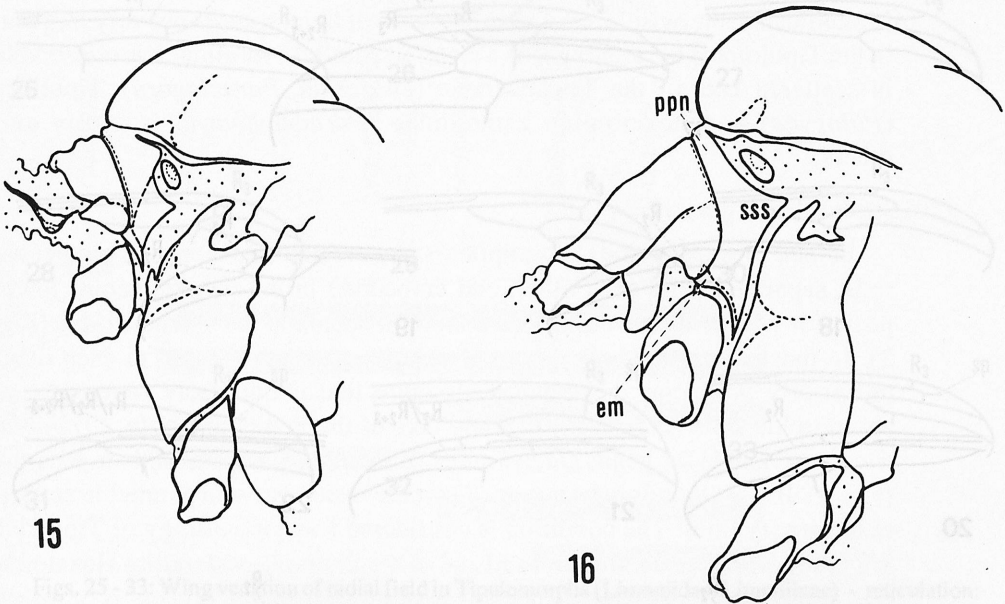


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Figs. 13 - 14: Anterior part of pleura in Tipulomorpha: 13 - *Dactylolabis* (s. str.) *transversa* MEIG. (Limoniidae: Dactylolabinae); 14 - *Euphyllidorea fulvonervosa* SCHUMM. (Limoniidae: Hexatomiinae). sss - subspiracular sclerite; for further abbreviations, see Figs. 9 - 10.

A depression or fold indicating the border between this sclerotized area and the strip-like pleural part of the postpronotum (Figs. 13-15) may be completely obliterated in more specialized taxa (Limoniinae; Fig. 16). Having not found any name for the element in the literature and considering its phylogenetic (and actually also taxonomic) significance, I term it here the "subspiracular sclerite", sss. The presence of the subspiracular sclerite represents a strong synapomorphy of all subfamilies of the Limoniidae, in the present restricted sense, excluding the former "Pediinae".

Through the subspiracular sclerite, the pleural part of the postpronotum becomes broadly attached to, or rather fused with, the prothoracic epimeron, em (Figs. 14-16), the latter being mostly delimited by somewhat darker colouration only. Whereas, in the Hexatomiinae and Eriopterinae, a more or less pronounced incision, indicating the fusion line, is observable on the posterior margin of the sclerites, in the Limoniidae, the margin is even, free of any incision or nick and the epimeron is traceable only as a narrow arched darker strip over the coxa (Fig. 16). The broad attachment or fusion of the epimeron to the subspiracular sclerite is another aspect of the above-described apomorphic condition. In the Trichoceridae, Pediciidae, Tipulidae and Cylindrotomidae, the epimeron is present in its plesiomorphic state, i.e. as a separate sclerite mostly attached to the episternum and at most in point contact with the pleural part of the postpronotum (Figs. 9-12). Whether the deep incision separating the subspiracular sclerite from the epimeron in *Dactylolabis* (Limoniidae; Fig. 13)

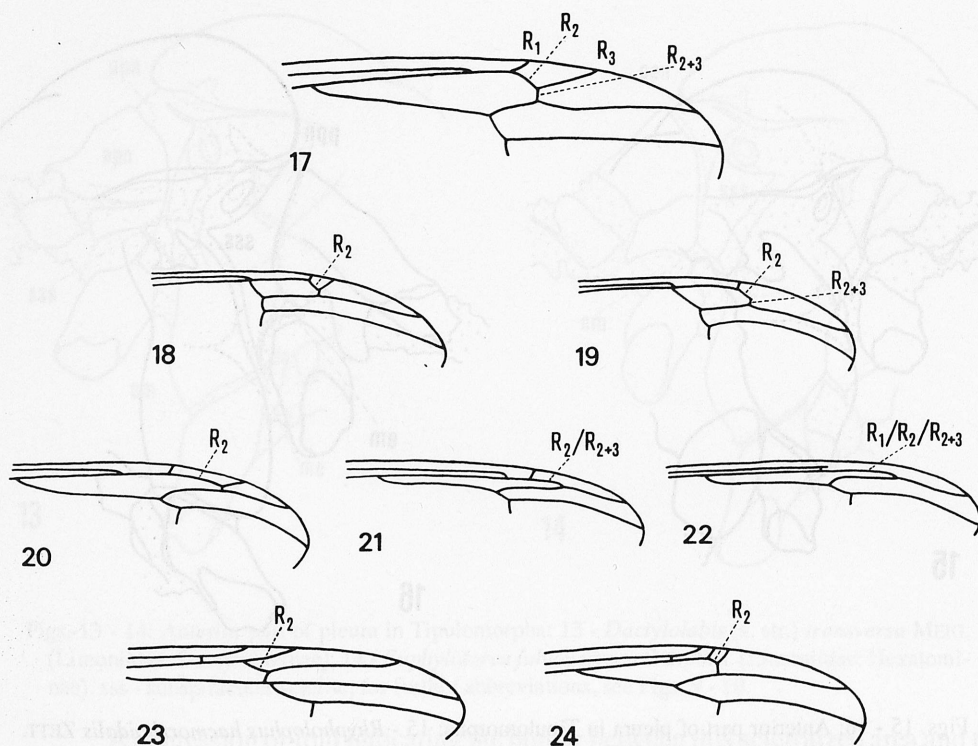


Figs. 15 - 16: Anterior part of pleura in Tipulomorpha: 15 - *Rhypholophus haemorrhoidalis* ZETT. (Limoniidae: Eriopterinae); 16 - *Limonia nubeculosa* MEIG. (Limoniidae: Limoniinae). For abbreviations, see Figs. 9 - 10 and 13 - 14.

represents a link to the fusion of the sclerites, or is a result of secondary reduction, remains so far in question.

(7) Outer dististyle of male terminalia strongly sclerotized.

Male genitalia are mostly too specialized structures to be useful for phylogenetic considerations at higher levels. However, one peculiarity appears to be significant at the subfamily level in the Limoniidae. In the Trichoceridae, a single pair of fleshy, unpigmented dististyles is present and this condition is likely to represent the ground plan character of the infraorder. The remaining families are apomorphic in that dististyle is divided into two portions called the inner and outer dististyle, though the modifications are frequent. Within the Limoniidae this character in its more primitive expression is exhibited in the genus *Dactylolabis* in which two pairs of fleshy, unpigmented and obtuse dististyles occur, whereas, in the subfamilies Hexatominæ, Eriopterinae and Limoniinae, the outer dististyle is strongly sclerotized and pointed apically. This latter condition is considered a synapomorphy of the three subfamilies. Of course, it is very often modified and obscured by further development, including secondary desclerotization of the outer dististyle or even its full atrophy, but relevant taxa always can be linked with the ground plan condition on the basis of other features.

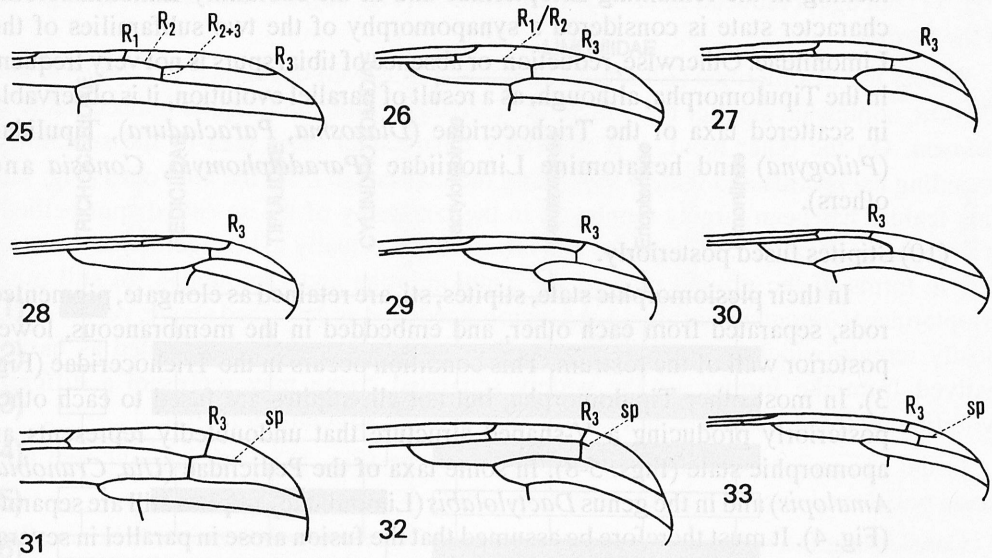


Figs. 17 - 24: Wing venation of radial field in Tipulomorpha - reticulation: 16 - *Dictenidia bimaculata* L. (Tipulidae) (after SAVCHENKO 1973); 18 - *Dolichopeza (Trichodolichopeza) dingaan* ALEX. (Tipulidae) (after ALEXANDER 1960); 19 - *Dolichopeza (Trichodolichopeza) senzangakono* ALEX. (Tipulidae) (after ALEXANDER 1960); 20 - *Phalacrocera replicata* L. (Cylindrotomidae) (after ALEXANDER 1927); 21 - *Phalacrocera minuticornis* ALEX. (Cylindrotomidae) (after ALEXANDER 1935); 22 - *Phalacrocera manipurensis* ALEX. (Cylindrotomidae) (after ALEXANDER 1964); 23 - *Conosia irrorata* WIED. (Limoniidae: Hexatominae) (after ALEXANDER 1927); 24 - *Protohelius issikii* ALEX. (Limoniidae: Limoniinae) (after ALEXANDER 1928).

(8) Reticulation of radial veins.

"Reticulation"*, a venational pattern as termed here, evolved through the distalization of the branching point R₂₊₃ - R₄ towards the verticalized R₂, combined with the proximalization of R₁ (for evolution of wing venation, see (1)). Vein R₂, appearing as if drawn back by the retracting R₁, occupies an oblique or longitudinal position and the participating elements, i.e. distal section of R₁, veins R₂₊₃, R₂ and R₃, arrive, in standard cases, at a more or less reticulate arrangement. (Figs. 17, 18, 24). Reticulation is clearly an apomorphic state achieved in accordance with the principal tendencies in the evolution of wing venation in the Tipulomorpha, as outlined under (1). It represents a synapo-

*The term is not to be related to the reticulation theory by Hardy (1951).



Figs. 25 - 33: Wing venation of radial field in Tipulomorpha (Limoniidae: Limoniinae) - reticulation: 25 - *Orimarga* (s. str.) *excessiva* ALEX. (after ALEXANDER 1927); 26 - *Orimarga* (s. str.) *virgo* ZETT. (after SAVCHENKO 1985); 27 - *Limonia nigropunctata* SCHUMM. (after SAVCHENKO 1985); 28 - *Libnotes* (*Afrolimonia*) *discoboloides* ALEX. (after ALEXANDER 1974); 29 - *Dicranomyia* (s. str.) *didyma* MEIG. (after SAVCHENKO 1985); 30 - *Libnotes* (*Paralibnotes*) *bidentoides* ALEX. (after ALEXANDER 1972); 31 - *Dicranomyia tristigmata* ALEX. (after ALEXANDER 1927); 32 - *Achyrolimonia decemmaculata* LOEW (after SAVCHENKO 1985); 33 - *Thrypticomysia doddi* ALEX. (after ALEXANDER 1927). sp. - "vein spur".

morphy of Tipulidae + Cylindrotomidae and evolved in parallel in the subfamily Limoniinae (except for the genus *Lipsothrix*). Exceptionally, the condition is observable also in other Limoniidae (eg. Hexatominiae: *Conosia*, Fig. 23). In most Cylindrotomidae and in some Tipulidae (some *Dolichochepeza*, *Scamboneura*), the typical appearance of the pattern is obscured by further apomorphic modifications, namely the atrophy of R3 (Figs. 19, 21) and sometimes even of the distal section of R1 (Fig. 22). Similarly, in the Limoniinae, except for some aberrant cases (some *Lechria* and *Trentepohlia*), the reticulation process is continued in alignment of the proximal section of R1 and veins R2 and R3. In the latter subfamily, however, the atrophy of the distal section of R1 precedes the atrophy of R3. Thus, a condition arises indistinguishable from, and convergent to, standard venational patterns in other subgroups of the family Limoniidae (Figs. 25-33).

(9) Tibial spurs reduced or absent.

Although not so striking as in some other nematoceran families, tibial spurs, situated at the distal ends of the tibiae, mostly are fairly well developed in the Tipulomorpha; their ground plan formula is 1:2:2. They are reduced in size in some primitive ecriopterine Limoniidae (*Neolimnophila* and allies) and entirely

lacking in the remaining Eriopterinae and in the subfamily Limoniinae. This character state is considered a synapomorphy of the two subfamilies of the Limoniidae. Otherwise, reduction or absence of tibial spurs is not very frequent in the Tipulomorpha, although, as a result of parallel evolution, it is observable in scattered taxa of the Trichoceridae (*Diazosma*, *Paracladura*), Tipulidae (*Ptilogyna*) and hexatomine Limoniidae (*Paradelphomyia*, *Conosia* and others).

(10) Stipites fused posteriorly.

In their plesiomorphic state, stipites, sti, are retained as elongate, pigmented rods, separated from each other, and embedded in the membranous, lower posterior wall of the rostrum. This condition occurs in the Trichoceridae (Fig. 3). In most other Tipulomorpha, but not all, stipites are fused to each other posteriorly producing a V-shaped structure that undoubtedly represents an apomorphic state (Figs. 5-8). In some taxa of the Pediciidae (*Ula*, *Crunobia*, *Amalopsis*) and in the genus *Dactylolabis* (Limoniidae), stipites still are separate (Fig. 4). It must therefore be assumed that the fusion arose in parallel in several evolutionary lines. The condition is considered a synapomorphy of Tipulidae + Cylindrotomidae on the one hand and of the limoniid subfamilies Hexatominae, Eriopterinae and Limoniinae on the other. The fusion process is probably combined with overall reduction of the structure because, if fused, stipites are generally less pigmented and distinct than in their plesiomorphic unconnected state, sometimes becoming hardly distinguishable. They are further modified in shape and position in connection with the prolongation of the rostrum and sclerotization of its lower wall (e.g., in the Tipulidae and in *Helius*, *Elephantomyia* and others of the Limoniidae).

(11) Media with three branches, M₁ and M₂ fused.

Normally, 4 medial veins which reach the wing margin, are present in the Tipulomorpha. Distalization of the fork M₁-M₂ belongs to principal evolutionary trends manifested throughout the infraorder and fusion of M₁ with M₂ was completed in parallel in different phylogenetic lines. In nearly all groups, scattered taxa occur in which this apomorphy was achieved. This character state appears to be of some phylogenetic value in the eriopterine and limoniine Limoniidae where it is nearly constant, the only exception being the group of genera centering *Neolimnophila*.

Distribution within the Tipulomorpha of the above all characters, with corresponding numbers, is illustrated in Fig. 34.

As already mentioned, many additional characters were checked. However, they proved not to be useful for phylogenetic considerations at family or subfamily levels. These characters will not be enumerated but attention is paid here to one which commonly was used in the systematics of the Tipulomorpha, namely the shape of meron.

Meron, me, is represented as a distinct, solid and well-sclerotized sclerite in *Trichocera* (Trichoceridae) (Fig. 9) and this obviously is to be regarded as the plesiomorphic state. A

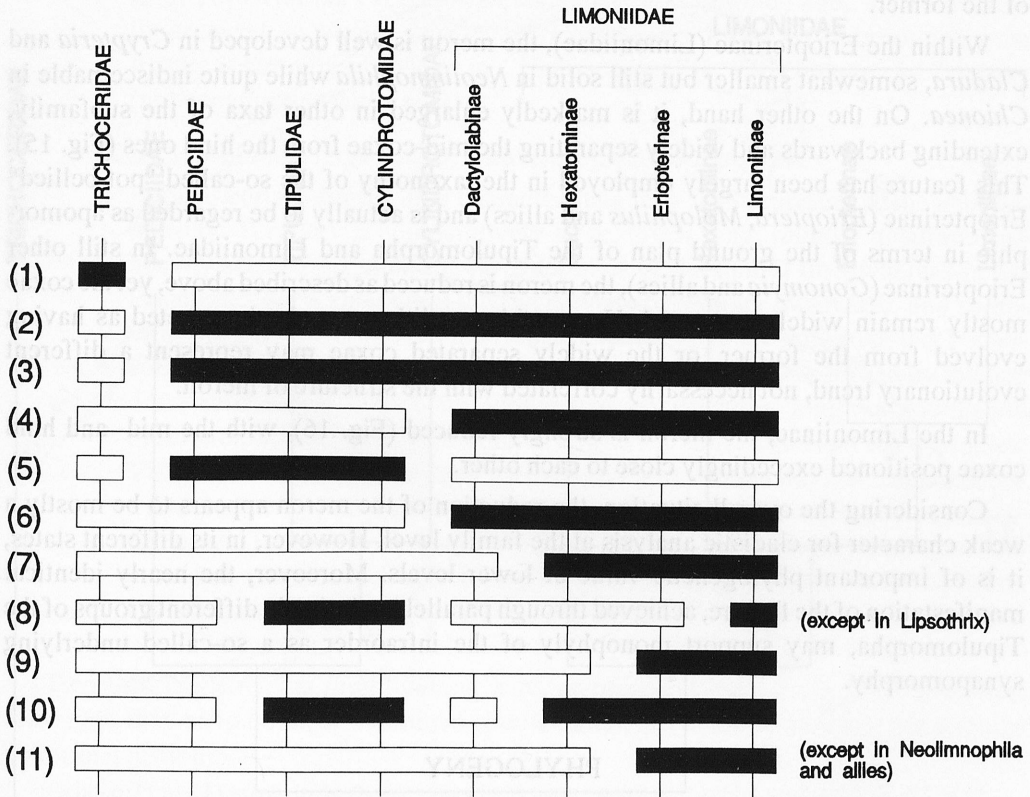


Fig. 34: Distribution of characters among main groups of Tipulomorpha. The numbers correspond to those given in the text for individual characters (chapter "Characters"). Solid rectangles - synapomorphies; hollow rectangles - symplesiomorphies.

similar condition may be seen in the Tipulidae (Fig. 11) and some eriopterine Limoniidae (Fig. 15). In all the other tipulomorph taxa, the meron is reduced in nearly the same way, i.e., that two, small, roughly triangular and sometimes coupled plates remain, attached to the posterior margin of the mid-coxa, while the rest of the area is membranous (Figs. 10, 12-14, 16). In addition, a minute strip is sometimes observable, attached to the mesothoracic katepimeron which, likewise, seems to be a component of the meron (Figs. 10, 14, 16). Shared possession of this feature in a strikingly similar expression in different groups of the Tipulomorpha gave rise to an idea that this might be a strong synapomorphy. This presumption proved, however, to be false. A reduced meron occurs even in taxa which otherwise are linked (by so many features) to groups where the meron is retained in its plesiomorphic state, that there is no doubt that the condition must have evolved several times through parallel evolution.

So, for instance, within the Trichoceridae, the meron is reduced in *Diazosma* and *Paracladura*, but retained in *Trichocera* (Fig. 9). In the Tipulidae, it is fully developed

(Fig. 11) but again reduced in the Cylindrotomidae (Fig. 12), the undoubted sister group of the former.

Within the Eriopterinae (Limoniidae), the meron is well developed in *Crypteria* and *Cladura*, somewhat smaller but still solid in *Neolimnophila* while quite indiscernable in *Chionea*. On the other hand, it is markedly enlarged in other taxa of the subfamily, extending backwards and widely separating the mid-coxae from the hind ones (Fig. 15). This feature has been largely employed in the taxonomy of the so-called "pot-bellied" Eriopterinae (*Erioptera*, *Molophilus* and allies) and is actually to be regarded as apomorphic in terms of the ground plan of the Tipulomorpha and Limoniidae. In still other Eriopterinae (*Gonomyia* and allies), the meron is reduced as described above, yet the coxae mostly remain widely separated. Hence, this condition may be interpreted as having evolved from the former, or the widely separated coxae may represent a different evolutionary trend, not necessarily correlated with the structure of meron.

In the Limoniinae, the meron is strongly reduced (Fig. 16), with the mid- and hind coxae positioned exceedingly close to each other.

Considering the overall situation, the reduction of the meron appears to be mostly a weak character for cladistic analysis at the family level. However, in its different states, it is of important phylogenetic value at lower levels. Moreover, the nearly identical manifestation of the feature, achieved through parallel evolution in different groups of the Tipulomorpha, may support monophyly of the infraorder as a so-called underlying synapomorphy.

PHYLOGENY

The phylogeny suggested here (Fig. 35) results from the analysis of adult morphological characters (see "Characters"), supported by further features (see below). The Tipulomorpha, as conceived in this paper, i.e., including the family Trichoceridae, are thought to have evolved along two phylogenetic lines. The one line, with shortened A₂, separate and well-developed cardo, and ocelli present, led to the Trichoceridae, which obviously are highly primitive and represent a relict group. The other line, in which A₂ may be characterized as "normal" in length, and cardines and ocelli are not distinguishable, gave rise to the other tipulomorph families.

This second line appears to be much more progressive. It separated into two main branches, the "tipulid" and "limoniid" lines. The tipulid line is thought to represent the ancestor of the Pediciidae, Tipulidae and Cylindrotomidae. As this conception, associating cladistically the former "Pediciinae" of the Limoniidae with the other two families, is newly introduced here, monophyly of this group represents a crucial point of the presumed phylogeny. It is therefore discussed here in some detail. The tipulid line is characterized by a reduced postpronotum, which is strongly impressed dorsally, and by further modifications of the anteppronotum and prescutum, as specified under (5) in "Characters". This is considered an apomorphy. Another feature characterizing the tipulid line is plesiomorphic; the pleural part of the postpronotum is narrow, strip-like, and tapering downwards, not enlarged by the subspiracular sclerite. To support the monophyly of the group the

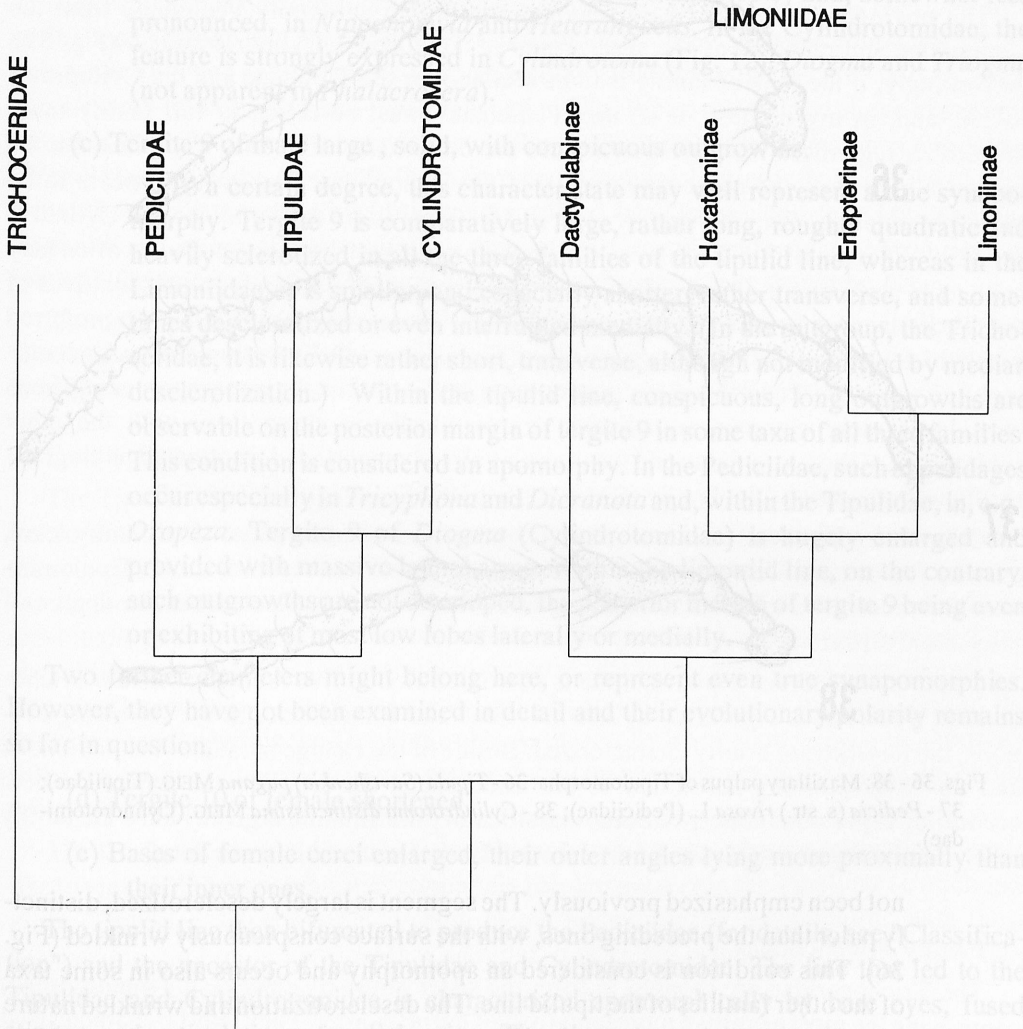
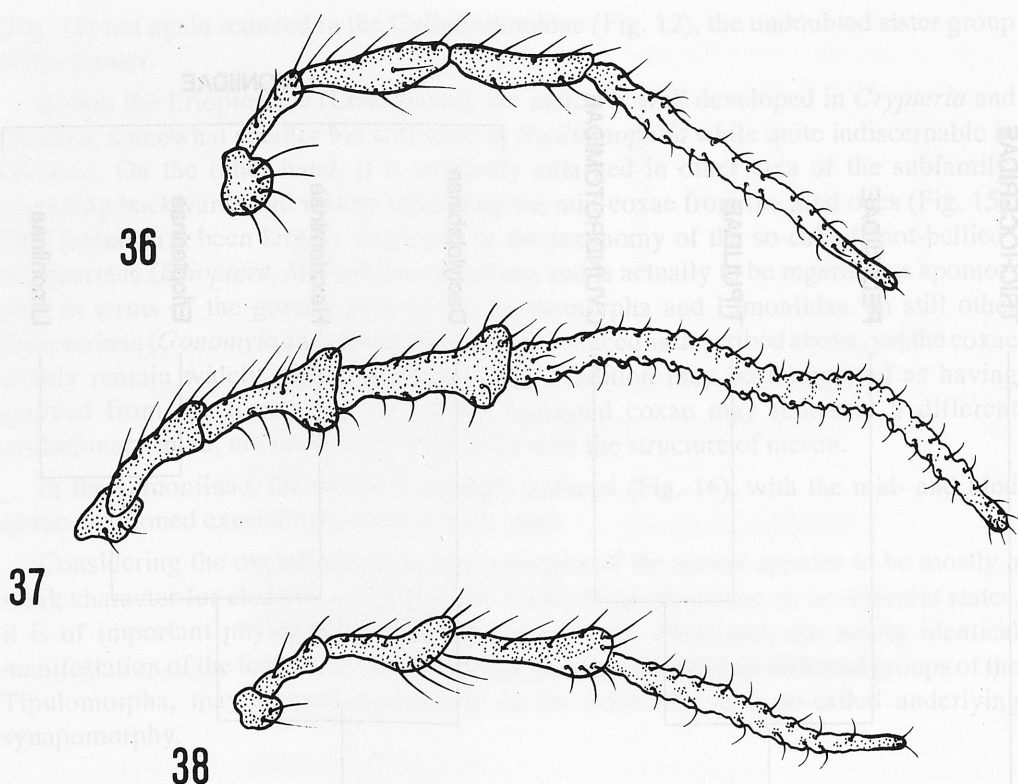


Fig. 35: Presumed phylogeny of Tipulomorpha.

following features may be pointed out which are observable in some taxa of each of the three families and may thus be regarded as agreement in capacity to develop parallel similarity (so-called underlying synapomorphy; cf. SAETHER 1979):

(a) Terminal palpal segment elongate and desclerotized.

This is one of the principal taxonomic features which generally is employed as diagnostic for the Tipulidae. The terminal palpal segment is conspicuously elongate throughout the family, somewhat more slender than preceding segments, and described as whip-like. However, another aspect of this feature has



Figs. 36 - 38: Maxillary palpus of Tipulomorpha: 36 - *Tipula* (*Savtshenkia*) *pagana* MEIG. (Tipulidae); 37 - *Pedicia* (s. str.) *rivosa* L. (Pediciidae); 38 - *Cylindrotoma* *distinctissima* MEIG. (Cylindrotomidae).

not been emphasized previously. The segment is largely desclerotized, distinctly paler than the preceding ones, with the surface conspicuously wrinkled (Fig. 36). This condition is considered an apomorphy and occurs also in some taxa of the other families of the tipulid line. The desclerotization and wrinkled nature of the segment appear more significant than its actual length. In the Pediciidae, the character is observable in, e.g., *Pedicia*, *Nipponomyia* and *Heterangaeus*. Whereas in the nominotypical subgenus *Pedicia* s. str., the segment is enormously elongate (Fig. 37), in relative length even exceeding the condition in most of the Tipulidae, in some species of the subgenus *Crunobia*, it is quite short, equal in length to the penultimate, yet of similar structure as described above, i.e., largely desclerotized and conspicuously wrinkled. Within the Cylindrotomidae, the character is best pronounced in *Cylindrotoma* (Fig. 38).

(b) Prescutum flattened.

The prescutum is fairly vaulted in a great amount of taxa of the tipulid line and, since it is so also in the outgroup, the Trichoceridae (Fig. 9), the condition is thought to be plesiomorphic. In the Tipulidae, the prescutum is distinctly

flattened (Fig. 11). As to the Pediciidae, a similar condition occurs in *Pedicia* (Fig. 10) (with the exception of the subgenus *Amalopis*) and, somewhat less pronounced, in *Nipponomyia* and *Heterangaeus*. In the Cylindrotomidae, the feature is strongly expressed in *Cylindrotoma* (Fig. 12), *Diogma* and *Triogma* (not apparent in *Phalacrocer*).

(c) Tergite 9 of male large, solid, with conspicuous outgrowths.

To a certain degree, this character state may well represent a true synapomorphy. Tergite 9 is comparatively large, rather long, roughly quadratic and heavily sclerotized in all the three families of the tipulid line, whereas in the Limoniidae, it is smaller, and especially shorter, rather transverse, and sometimes desclerotized or even interrupted medially. (In the outgroup, the Trichoceridae, it is likewise rather short, transverse, although not modified by median desclerotization.) Within the tipulid line, conspicuous, long outgrowths are observable on the posterior margin of tergite 9 in some taxa of all three families. This condition is considered an apomorphy. In the Pediciidae, such appendages occur especially in *Tricyphona* and *Dicranota* and, within the Tipulidae, in, e.g., *Oropeza*. Tergite 9 of *Diogma* (Cylindrotomidae) is hugely enlarged and provided with massive lateral arms. Within the limoniid line, on the contrary, such outgrowths are not developed, the posterior margin of tergite 9 being even or exhibiting at most low lobes laterally or medially.

Two further characters might belong here, or represent even true synapomorphies. However, they have not been examined in detail and their evolutionary polarity remains so far in question.

(d) Tergite 10 of female shortened.

(e) Bases of female cerci enlarged, their outer angles lying more proximally than their inner ones.

The tipulid line then bifurcated to produce the Pediciidae (for details, see "Classification") and the ancestor of the Tipulidae and Cylindrotomidae. The line that led to the Tipulidae and Cylindrotomidae is characterized apomorphically by bare eyes, fused stipites and reticulation of radial veins. The character states are, however, largely paralleled in the family Limoniidae. Further synapomorphy of the two families may be found in the structure of the head (lower wall of rostrum sclerotized; see also under "Tipulidae" in "Classification").

The other branch, termed here the limoniid line, gave rise to the family Limoniidae. Monophyly of the group is based on the following synapomorphies: presence of subspiracular sclerite, broadly attached or fused to the epimeron; flattened, elongate antepnotum; fused stipites; and sclerotized outer dististyle of the male genitalia (the two latter characters not shared by *Dactylolabis*) (see also under "Limoniidae" in "Classification"). Since the above monophyly is believed to be well supported, numerous underlying synapomorphies are not detailed here. The presumed phylogeny of the subfamilies of the Limoniidae is illustrated in Fig. 35 and argued below in "Classification" under particular taxa.

CLASSIFICATION

The phylogeny presented here removes the former subfamily Pediciinae from the Limoniidae and places it as the sister group of Tipulidae + Cylindrotomidae (Fig. 35). Accordingly, if the rank of family is to be retained for the Tipulidae and the Cylindrotomidae, and, in my opinion, it is, the "Pediciinae" must be raised to full family rank. Moreover, regardless the phylogeny, there are other reasons for the "Pediciinae" to be ranked higher than the other subfamilies of the Limoniidae. The group appears to be homogeneous one, characterized by clear-cut features, as are the Tipulidae and Cylindrotomidae. Whereas within the Limoniidae, in the present restricted sense, doubts often may arise as to assignment of individual genera to a particular subfamily, representatives of the "Pediciinae" are readily recognizable as such. Therefore, a classification is preferred here which secures the family rank for the Tipulidae and Cylindrotomidae and, accordingly, elevates the "Pediciinae" to the same category. Actually, the group has recently been considered more compact and distinct taxonomically in comparison with the other subfamilies of the Limoniidae and was even, as already mentioned, contrasted phylogenetically with the rest of the family (SAVCHENKO 1986).

Otherwise, of course, the above phylogeny can also be interpreted at subfamily level, ensuing from Alexander's conception accepted by American students of the Tipulomorpha. However, I believe that the former classification does reflect better the degree of taxonomic difference.

Thus, the infraorder Tipulomorpha is now classified in five families, viz. the Trichoceridae, Pediciidae, Tipulidae, Cylindrotomidae and Limoniidae. In the following sections, the families are briefly characterized. Beside of the change in rank of the Pediciidae and the corresponding restriction of the Limoniidae, the families are conceived here according to previous concepts. Some classificatory information is given below the family level. Subfamily classification of the Limoniidae is discussed in some detail.

Family Trichoceridae

The Trichoceridae are thought to form the sister group of remaining Tipulomorpha, comprising the most primitive representatives of the infraorder. They may be characterized by plesiomorphic features that are part of the ground plan of the Tipulomorpha, as discussed in "Characters" and shown in Fig. 34. The only ground plan apomorphy suggested is represented by the shortened A₂. There are, of course, numerous further characters that are of diagnostic value (e.g., wing venation, structure of the male and female terminalia) which, however, could not be employed in the cladistic analysis because of their clearly plesiomorphic nature or uncertain evolutionary polarity.

The family is delimited here in the common sense. As far as classification below family level is concerned, attention should be drawn to the fact that the genera *Diazosma* and *Paracladura* differ apomorphically from the ground plan of the family in that they have reduced tibial spurs and meron. This, possibly, is to be reflected in the classification at subfamily, or, rather, tribal level. In any case, the delimiting line cannot be placed between *Kawasemyia* and the other taxa.

Family Pediciidae

The Pediciidae constitute a homogeneous, clearly defined group that is regarded here as the sister group of Tipulidae + Cylindrotomidae. They may be characterized by pubescent eyes and spurred tibiae in combination with some venational characters, such as a strongly retracted Sc₂ and four-branched media. While most of the above characters are plesiomorphic, the strongly retracted Sc₂ undoubtedly represents an apomorphy. Overall shape of body, especially the thorax, and structure of the mouthparts and male and female terminalia may provide further apomorphies. In addition, some larval traits should be mentioned, above all, the narrowed compact head capsule and reduction in number of lobes on the spiracular disc. The latter character is, however, not shared by *Ula*.

The delimitation of the family is identical with that outlined previously for the former "Pediciinae". Separation into two subgroups, maybe tribes rather than subfamilies, appears sound, contrasting the genus *Ula* with the other taxa.

Family Tipulidae

The Tipulidae are thought here to form the sister group of the Cylindrotomidae, being linked with the latter by significant synapomorphies (see "Phylogeny"). They represent the second largest family of the Tipulomorpha. I am not familiar with all necessary details but the most important ground plan apomorphy of the Tipulidae seems to me to be exhibited by the structure of rostrum, which is elongate, with genal areas extended and closed beneath (Fig. 6). (In the Cylindrotomidae, the lower wall of rostrum likewise is largely sclerotized but not closed medially.) The so-called nasus at the distal end of the rostrum is unique within the Tipulomorpha. As the family is very homogeneous taxonomically, numerous diagnostic features may be found on nearly every part of body, including wing and male and female terminalia.

The family is conceived here in the traditional sense. Although not a specialist, I would like to remark that the subfamilies commonly recognized within the Tipulidae (Dolichopezinae, Tipulinae, Ctenophorinae) seem to me taxonomically incompatible with those proposed in the Limoniidae and that, in order to maintain balance in classification, they should rather be ranked as tribes.

Family Cylindrotomidae

As to number of species, the Cylindrotomidae represent the smallest of the tipulomorph families. They form the sister group of the Tipulidae. From the latter, they may readily be separated by a reduced meron, conspicuously shaped abdomen and by some peculiarities in wing venation. All the features may be evaluated as apomorphies. In addition, the shape of the larvae and their feeding habit likewise appear to be significant phylogenetically, representing an important autapomorphy (autopotypy) within the Tipulomorpha.

I am not familiar with structural details other than wing venation of the predominantly Oriental and Australian genera *Stibadocera* and *Stibadocerodes*. BRODO (1967) arranged them in the tribe Stibadocerini considering, however, the Cylindrotomidae a subfamily of the Tipulidae. Palearctic species of the family constitute a fairly homogeneous group.

Family Limoniidae

The Limoniidae are conceived here in the restricted sense, without the former "Pedi-cii-nae". They are thought to form the sister group of Pediciidae + Tipulidae + Cylindrotomidae and their taxonomic makeup is identical with that of the subfamily Limoniinae sensu lato, as suggested by SAVCHENKO (1986). The family is a rather diverse one, the largest of the Tipulomorpha and comprising the great majority of small and medium-sized crane-flies, in contrast to the sister group families which contain most of larger forms. Significant ground plan apomorphies of the Limoniidae appear to be a flattened antep-notum and presence of the subspiracular sclerite. These character states may well serve as diagnostic features, too. Further apomorphies include the fused stipites and sclerotized outer dististyle of the male genitalia (not shared by *Dactylolabis*).

The genus *Dactylolabis* is assigned the rank of subfamily. Hence, the Limoniidae, as delimited herewith, are classified in four subfamilies, the Dactylolabinae, Hexatominiae, Eriopterinae and Limoniinae. The present classification is deliberately conservative as far as some controversial cases are concerned. If more weight is attached to some characters, and the principle of ground plan characters more strictly applied, then further subfamilies could well be erected, namely for the group of genera centering around *Neolimnophila* and *Cladura* (including *Phyllolabis*), as the sister group of remaining Eriopterinae, and for the genus *Lipsothrix*, as the sister group of remaining Limoniinae (cf. Fig. 34).

In the following subsections, the subfamilies of the Limoniidae are briefly characterized. Some transfers of genera between the subfamilies are suggested that will indicate the delimitation presently accepted (already inferred in part from the above chapters), as compared with the concepts proposed by ALEXANDER and ALEXANDER (1973), or SAVCHENKO (1982, 1985, 1986, 1989).

Subfamily Dactylolabinae

The Dactylolabinae are thought here to represent the most primitive offshoot of the Limoniidae forming the sister group of Hexatominiae + Eriopterinae + Limoniinae. In relation to the other subfamilies, they may be characterized by plesiomorphies in the structure of stipites and the male genitalia, as described in "Characters" and shown in Fig. 34. Since, at the moment, only a single genus is included in the subfamily, it is somewhat difficult to point out apomorphies. They seem to be traceable in wing venation and female terminalia. Possibly, the deep incision separating the subspiracular sclerite from epimeron (Fig. 13), as mentioned in "Characters" under (6), might also prove to be an apomorphy. As to the larvae, shape of the body and their hygropetric way of life are likely to belong here, although the latter is paralleled in scattered taxa across the family.

Subfamily Hexatominiae

According to the presumed phylogeny, the Hexatominiae form the sister group of Eriopterinae + Limoniinae. In relation to the latter, they may generally be characterized by presence of fairly developed tibial spurs and a four-branched media. These character states represent plesiomorphies. Apomorphies are foreshadowed in some details of the

structure of the mesothoracic pleura (katepimeron divided by a suture) and female terminalia (tergite 10 expanded before insertion of cerci).

The concept of the subfamily, as suggested herewith, differs somewhat from that accepted previously. Beside the genus *Dactylolabis*, which is now segregated to constitute a separate subfamily, *Phyllolabis* and *Atarba* are to be placed in the Eriopterinae and *Elephantomyia* and *Helius* in the Limoniinae. On the other hand, the genus *Conosia* is to be transferred from the Eriopterinae into the Hexatominæ and the same is probably to be done with the related extralimital *Clydonodozus*.

Subfamily Eriopterinae

The subfamily is the largest one of the Limoniidae, comprising mostly small forms. It is regarded here as the sister group of the Limoniinae. The Eriopterinae may be characterized by lack of tibial spurs and by a three-branched media, combined with a well-developed meron. The two former features are clearly apomorphic but, on the one hand, shared by the Limoniinae, on the other, not fully pronounced in the group of genera around *Neolimnophila*. The latter character, though seemingly plesiomorphic, is considered here an apomorphy, too. The meron is markedly enlarged in a considerable amount of species (*Erioptera*, *Molophilus* and allies), extending backwards and widely separating the mid-coxae from the hind coxae. Another state of this character is observable in the group of genera centering around *Gonomyia*, eg. *Gnophomyia*, *Ellipteroides* and *Idiocera* (though not especially pronounced in *Gonomyia* itself), where the meron is reduced but coxae remain widely separated (see closing paragraphs in "Characters"). Thus, the shape of the meron, combined with the position of the coxae, as described above, represents not only a good diagnostic feature but is considered here an apomorphy of the subfamily (with some reservations as to *Neolimnophila* and allies). Another apomorphy, possibly correlated with the latter, may be that all coxae are more or less shortened, as compared with the condition in the other subfamilies. This feature should, however, be examined in detail.

As to the delimitation of the subfamily, some changes are suggested here, as compared with previous concepts. The genus *Conosia* (and possibly also *Clydonodozus*) is to be transferred from the Eriopterinae into the Hexatominæ. The genera *Lipsothrix*, *Trentepohlia* and *Dicranoptycha* should be removed from the Eriopterinae and placed in the Limoniinae. In contrast, the genera *Phyllolabis* and *Atarba* are regarded here as representatives of the Eriopterinae.

Subfamily Limoniinae

The Limoniinae are considered here the sister group of the Eriopterinae. As with the latter subfamily, they likewise may be characterized by a lack of tibial spurs and by a three-branched media, this, however, in combination with a strongly reduced meron. Remnants of the sclerite are quite minute (Fig. 16), with the mid- and hind coxae being situated exceedingly close to each other. This is clearly a highly apomorphic step, best observable on fresh material. Another apomorphy of the Limoniinae, which, moreover, can be used as a diagnostic feature, is the entirely coalescent pleural part of the postpronotum and the subspiracular sclerite, with no depression or fold separating them (Fig. 16,

see also "Characters" under (6)). The so-called reticulation of the radial veins (see "Characters" under (8) and Figs. 25-33) likewise belongs here although it is paralleled in the Tipulidae and Cylindrotomidae, and not shared by *Lipsothrix*. Unfortunately, in most of genera, this character state is not easily discernible, being obscured by further apomorphic development (see "Characters" under (8)).

The present concept of the subfamily warrants some systematic shifts, as compared with previous views. The following genera should be included: from the Hexatomininae: *Elephantomyia* and *Helius*; from the Eriopterinae: *Lipsothrix*, *Trentepohlia* and *Dicranoptycha*. Examination of some extra-Palaeartic taxa revealed that *Lechria*, *Tonnoiro-myia*, *Xipholimnobia* and *Toxorhina* are likewise to be regarded as representatives of the subfamily.

NOMENCLATURAL NOTE

According to the International Code of Zoological Nomenclature (1985) "The valid name of a taxon is the oldest available name applied to it ..., provided that that name is not invalidated by any provision of the Code or by ruling of the Commission". (Article 23(a)). The provision must naturally be applied to family-group names, too.

Two family-group names used in this treatment should be replaced by their senior synonyms. The subfamily Hexatomininae of the Limoniidae is to be named the Limnophilinae and the subfamily Eriopterinae of the same family the Chioneinae. Selected synonymy of the two taxa is provided herewith.

Limnophilinae

Limnophilidae BIGOT, 1854, *Annls Soc. ent. Fr.*, (3)2:466.

Limnophilina; OSTEN SACKEN, 1869, *Smithson. misc. Collns*, 8(219):23.

Anisomerina OSTEN SACKEN, 1869, *Smithson. misc. Collns*, 8(219):23.

Limnophilinae; VERRALL, 1886, *Entomologist's mon. Mag.*, 22:118.

Anisomerinae; VERRALL, 1886, *Entomologist's mon. Mag.*, 22:118.

Anisomerinae; KERTÉSZ, 1903, *Katalog Paläarkt. Dipt.*, 1:314.

Limnophilini; ALEXANDER, 1912, *Ent. News*, 23:67.

Anisomerini; ALEXANDER, 1912, *Ent. News*, 23:67.

Hexatomini ALEXANDER, 1914, *Psyche*, 21:33.

Chioneinae

Chioneinae RONDANI, 1841, *Nuovi Annali Sci. Nat.*, (6)3:284.

Chionidae; BIGOT, 1854, *Annls Soc. ent. Fr.*, (3)2:466.

Eriopterina OSTEN SACKEN, 1869, *Smithson. misc. Collns*, 8(219):23.

Eriopterinae; VERRALL, 1886, *Entomologist's mon. Mag.*, 22:118.

Eriopterinae; KERTÉSZ, 1903, *Katalog Paläarkt. Dipt.*, 1:289.

Eriopterini; ALEXANDER, 1912, *Ent. News*, 23:67.

There are further inconsistencies in the nomenclature of the Limoniidae at the family-group level. They will have to be solved in the future. To avoid this at present, intentionally, no tribal names are cited in the present paper.

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